Soil water-holding capacity and monodominance in Southern Amazon tropical forests

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Abstract

Background and Aims

We explored the hypothesis that low soil water-holding capacity is the main factor driving the monodominance of *Brosimum rubescens* in a monodominant forest in Southern Amazonia. Tropical monodominant forests are rare ecosystems with low diversity and high dominance of a single tree species. The causes of this atypical condition are still poorly understood. Some studies have shown a relationship between monodominance and waterlogging or soil attributes, while others have concluded that edaphic factors have little or no explanatory value, but none has accounted for soil-moisture variation other than waterlogging. This study is the first to explicitly explore how low soil water-holding capacity influences the monodominance of tropical forests.

Methods

We conducted in situ measurements of vertical soil moisture using electrical resistance collected over one year at 0-5; 35-40 and 75-80 cm depths in a *B. rubescens* monodominant forest and in an adjacent mixed-species forest in the Amazon-Cerrado transition zone, Brazil. Minimum leaf water potential (Ψmin) of the seven most common species, including *B. rubescens*, and soil water-holding capacity for both forests were determined.

Results

The vertical soil moisture decay pattern was similar in both forests for all depths. However, the slightly higher water availability in the monodominant forest and Ψmin similarity between *B. rubescens* and nearby mixed forest species indicate that low water-availability does not cause the monodominance.

Conclusions

We reject the hypothesis that monodominance of *B. rubescens* is primarily determined by low soil water-holding capacity, reinforcing the idea that monodominance in tropical forests is not determined by a single factor.

Keywords soil moisture, monodominant species, water stress, soil gravel content, permanent wilting point, total porosity

Introduction

Monodominant forests are a rare forest type in the tropics (Hart et al. 1989) with low tree diversity, where 50 to 100% of the canopy is formed by individuals of a single species (Connell and Lowman 1989). Some factors have been attributed to explain the monodominance, but its determinants are still not well understood. Some authors described causes related to mycorrhizae association with the monodominant species (Connell and Lowman 1989, Marimon et al. *in press*), toxic elements released during litter layer decomposition (Villela and Proctor 2002), persistent seedling bank of monodominant species (Nascimento and Proctor 1997; Marimon et al. 2012), disequilibrium of Ca/Mg ratio in soil (Nascimento et al. 1997; Marimon et al. 2001; Nascimento et al. 2017) or even a set of multiple ecological conditions acting together (Marimon 2005; Peh et al. 2011a,b).

Other studies, which explore plant-soil-water interactions, have shown a clear relationship between monodominance and seasonal water saturation of soil, especially by waterlogging in hyperseasonal wet environments (see Arieira and Cunha 2006). However, there is no work to date investigating the opposite situation, where the monodominance could be a result of soil moisture restrictions in seasonal forests caused by low water-holding capacity of the soil (WHC). The studies comparing mixed and monodominant forests in similar edaphic conditions do not take soil moisture variations into account (e.g. Connell and Lowman 1989; Marimon et al. 2001; Peh et al. 2011a; Nascimento et al. 2017).

Several ecological studies in the tropics lend support for expecting this plant-soil-water relationship to drive floristic composition changes. In the pioneering work of Condit et al. (1996), shifts from wetter to drier environment were noted to cause changes in the dominance of tree species in a tropical forest in Panama. Similar wet-dry shifts in the tree species dominance were recorded in tropical forest by Butt et al. (2014). In southern Amazonia, long-term plot records show that more dry-affiliated tree genera (Esquivel-Muelbert et al. 2017) are now becoming more abundant because of drier conditions (Esquivel-Muelbert et al. 2018), while work elsewhere suggests soil moisture conditions and species hydraulic properties may govern plant drought vulnerabilities and marked floristic shifts (e.g., Feng et al. 2017). Therefore, we hypothesize that well-drained soils with low WHC in seasonal environments may cause severe water restrictions on plants and favour the monodominant species with higher drought resilience strategies. This may be the case for the monodominant *Brosimum rubescens* (Moraceae) forest in southern Amazonia, in which the high soil gravel concentration and possible low WHC (*sensu* Reynolds et al. 2000) can induce water stress more quickly (Richards & Weaver 1944; Dunne & Wilmot 1996). If the monodominant species has more drought resistance traits than the others, then it may gain a distinct competitive advantage, potentially leading to monodominance.

This hypothesis may complement that of Peh et al. (2011b) in which 'classical monodominance' is a condition not attained by a single factor, but a group of traits under long-term low environmental disturbance giving rise to a sequence of positive feedbacks favouring the monodominant species in tropical forests (*sensu* Connel and Lowman 1989). Therefore, low soil WHC, coupled with a set of ecological conditions, could be a conceptually attractive factor for favouring monodominance in seasonal and well-drained sites, such as those in concretionary (gravel) or sandy soils frequently found in the Amazonia/Cerrado boundary region. Indeed, species distribution and dominance in many tropical forests is known to be driven by sharp soil moisture variation (Furley 1992; Rodrigues 1992; Walter 1995; Silva-Júnior 1997; Ivanauskas et al. 1997; Rodrigues and Shepherd 2000) or even subtle variations throughout the year, as demonstrated by Marimon et al. (2003) and Marimon-Junior and Haridasan (2005) in the Amazonia/Cerrado transition region. Tree dominance is also related to drainage patterns (Sampaio et al. 2000), which act as a functional pathway (Pinto and Oliveira-Filho 1999) where better soil-moisture conditions between along riparian environments drives the flora distribution (Neiman et al. 1993). Similarly, plant available water heterogeneity in soil was one of the most important factors driving plant dominance at the horizontally scale of tens of meters in a Cerrado (Brazilian savanna) in Central Brazil (Ferreira et al. 2007).

Besides its influence on floristic variation and dominance within the same phytophysiognomy, soil hydrology also controls the distribution of whole vegetation types in diverse environmental conditions. Furley and Ratter (1990), for example, in studies conducted on

the Ilha de Maracá in Roraima, Amazonia, found evidence that soil hydrology, as opposed to soil fertility, was the main factor determining the distribution of vegetation types. Similarly, Marimon-Junior and Haridasan (2005) concluded that high clay content and its associated higher WHC, could be more important than soil fertility for determining the distribution of Cerradão vegetation (forest *facies* of Cerrado) in the Amazon/Cerrado transition zone. Durigan and Ratter (2006) also found a gradient of cerrado-forest vegetation associated with soil WHC in the South-eastern region of Brazil.

Hydrological conditions associated with monodominant forests are unclear. In some cases, a shallow water table is the principal determinant of the monodominance, as in the case of *Vochysia divergens* in the Pantanal of Mato Grosso (Nascimento and Cunha 1989) or *Mora excelsa* in Guyana (Davis and Richards 1934). On the other hand, *Peltogyne gracilipes* forest on the Ilha de Maracá (Nascimento et al. 1997, Nascimento and Proctor 1997), *Celaenodendron mexicanum* in Mexico (Martijena 1998), *Dicymbe corymbosa* in Guyana (Henkel 2003) and *Gilbertiodendron dewevrei* in Africa (Peh et al. 2011a) are not associated with waterlogging or swampy soil conditions. Therefore, flooding in some situations is strongly associated with monodominance, but in other cases it is not.

In contrast, soils that have a lower water retention capacity throughout the soil profile are less capable of supplying water for plants (Nye and Tinker 1977; Caldwell and Richards 1986), which may influence the species distribution in the environment (see Furley and Ratter 1990; Marimon-Junior and Haridasan 2005, Cosme et al. 2017, Zuleta et al. 2018), including hydrological niche segregation (Brum et al. 2018). In these situations, tree species better adapted to water stress in seasonal environments (e.g. Oliveira et al. 2018), could be superior competitors, prevailing among the others or even reaching monodominance. To assess if soil water restrictions are in fact related to monodominance of *B. rubescens*, we evaluated, in the laboratory and in the field, the variation in soil moisture over a year and the minimum leaf water potential (Ψmin) of *B. rubescens* and the six other main tree species according to the Importance Value Index (IVI) in a monodominant *Brosimum* forest (BF) and in an adjacent mixed forest (MF) in the transition zone between the Cerrado and the Amazon.

Our objective was to test whether hydrological restrictions in the concretionary soil (gravel), potentially induced by the higher soil gravel content of the BF (38.6%) compared to MF (28.5%), could act as an environmental filtering of species favouring *B. rubescens* to the detriment of others. Thus, our main question is whether the restriction of soil-moisture is part of the set of conditions that lead to monodominance. This assumption is based on previous works of Esquivel-Muelbert et al. (2017, 2018) that revealed the influence of environmental moisture conditions on the dominance of tree species across a precipitation gradient within the Amazon. We hypothesized that tree species better adapted to water stress in a seasonal environment could be superior competitors, prevailing among the others (Esquivel Muelbert et al. 2017, 2018) or even reaching monodominance. Therefore, the soil hydraulic restrictions in BF caused by lower water holding capacity results in conditions permitting monodominance of *B*. *rubescens*, which we expect to be a better competitor under edaphic water stress given the prior knowledge that the long-term success (dominance and change) of Amazon species is associated with moisture conditions (Esquivel-Muelbert et al. 2017, 2018). This study is the first to examine if seasonal restrictions in soil moisture, as opposed to complete waterlogging, may help explain the monodominance of a tropical forest.

Material and methods

Study sites

The study was conducted in a reserve of the Vera Cruz farm, municipality of Nova Xavantina-MT. The monodominant *Brosimum rubescens* forest (BF) and the adjacent mixed-species forest (MF) are located in the same fragment remaining of native forest. The coordinates of the BF are 14º50’47’’ S and 52º08’37’’ W and those of the MF are 14º49’32’’ S and 52º06’20’’ W. The climate is classified as seasonal Aw by Köppen, with four months of dry season (May to September) with monthly precipitation <100 mm. Annual precipitation ranges from 1300 to 1600

mm and mean monthly temperature is 25ºC according to the climatological station of the State University of Mato Grosso (UNEMAT), Nova Xavantina, Brazil (Fig. 1).

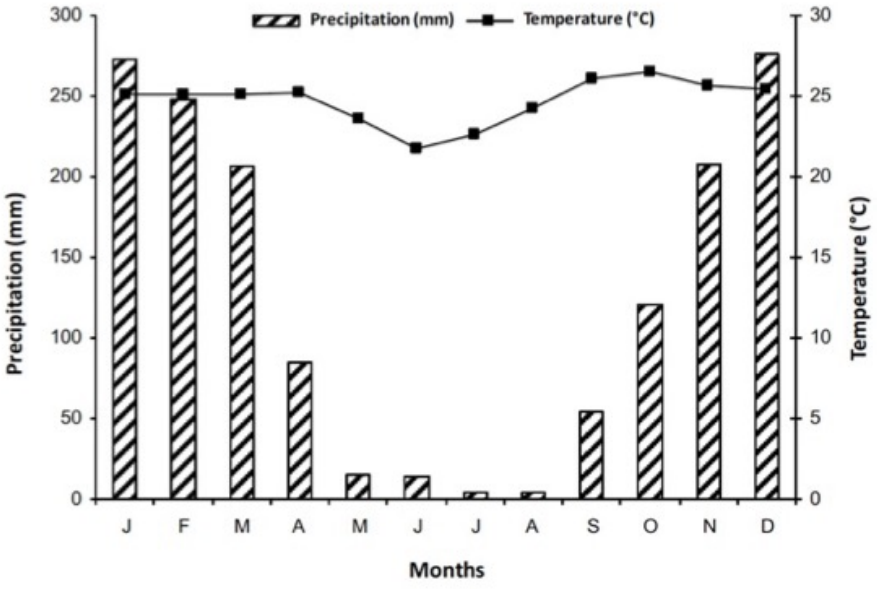

Figure 1. Monthly precipitation and temperature (mean daily basis) near the location of the Brosimum rubescens monodominant forest (BF) and an adjacente mixed forest (MF). Climate data from 1st January 2005 and 31 december 2006. Nova Xavantina meteorological station – INMET (National Institute of Meteorology).

The soil in both forests is a concretionary (gravel) Petric Plintosol (FAO) (Petroferric Acrustox, USDA taxonomy), strongly dystrophic (very low exchangeable bases) and alic (Al >2 $cmol_{(+)}\ kg^{-1}$), having more than 28% of gravel in the top 10 cm (Table 1). This value progressively increases until it forms an almost continuous semi-concretionary rock of hydromorphic laterite at approximately 90 cm depth. Despite some physico-chemical similarities, the soil in the BF has lower pH, much higher Al, much lower Ca and Mg, lower Mn and very high Mg/Ca ratio (Table 1). Our analysis is based on 60 permanent plots (10 x 10m, 0.01 ha) in both the BF, established in 1996 (Marimon et al. 2001), and in the MF, established in 2003 (Marimon 2005). The minimum tree diameter of inclusion is 10 cm measured at 1.3 m above the ground (DBH), or above any buttresses, in accordance with the RAINFOR protocol (e.g., Peacock et al. 2007). All plots were recensused in 2006 and 2010, with *B. rubescens* remaining strongly monodominant in the BF throughout (Marimon et al. 2012). In the BF, the monodominant species has an importance value index (IVI) much higher than the sum of the IVI of the next nine most important tree species, along with having a greater height and diameter and representing 80 % of total aboveground biomass (Marimon 2005). In the MF, the 10 species with the greatest importance values represent only 58% of the total, and *Cheiloclinium cognatum*, the most important species, contributes slightly less than 8% of the total basal area in this forest. The total biomass of BF and MF are estimated respectively as 479 and 238 Mg ha^{-1} based on a 2005 re-census (Marimon et al. 2014). The basal area (relative dominance) of *B. rubescens* in monodominant forest is 78,2% (dm >5cm) and only 1,8% in the MF (Marimon 2005).

Table 1 Percentage of gravel and chemical properties of the soils (0 to 10cm) of a monodominant *B. rubescens* forest (BF) and an adjacent mixed forest (MF), Nova Xavantina-MT. Differences between forests were determined using a t-test. The values are means and standard deviations. Adapted from Marimon (2005).

Forest	CEC	V	Grav	pH	pH	Al	Ca	Mg	K	Mg/	P	Fe	Mn
	($cmol_{(+)}\ kg^{-1}$)	(%)	(%)	H_2O	KCl	($cmol\ (+)\ kg^{-1}$)				Ca	($mg\ kg^{-1}$)		
BF	2.7	18.5	38.6	4.26	3.68	2.20	0.07	0.21	0.22	3.50	2.88	240.6	16.9
			(18.9)	(0.10)	(0.10)	(0.36)	(0.07)	(0.17)	(0.06)	(1.14)	(0.90)	(25.3)	(7.9)
MF	2.7	72.5	28.5	5.00	4.03	0.74	0.66	1.09	0.21	1.80	3.18	87.7	42.7
			(19.0)	(0.18)	(0.14)	(0.25)	(0.35)	(0.47)	(0.05)	(0.90)	(0.92)	(25.6)	(20.1)
P	-	-	**	***	**	***	***	***	n.s.	***	n.s.	***	***

CEC (cation exchange capacity) and V(%) (base saturation) were determined following Mello *et al.* (1985) and the others according to Tan (1996). The nutrients concentrations shown were obtained by the Mellich II method, where only extractable elements are determined. Grav= gravel; n.s.= no significant difference; ** = $p \leq 0{,}01$ and *** = $p \leq 0{,}0001$.

Field Studies

In situ soil moisture in both forests was estimated by electrical resistance using the method of Tan (1996), with bipolar electrodes encased in gypsum blocks (Hillel 1971). The sensors and equipment were manufactured by Eijkelkamp-Agrisearch Equipment, model *Soil Moisture Meter* 14.22.

In each area we installed probes at 10 randomly chosen measurement points. At each point sensors were inserted at three depths: 0-5, 35-40, and 75-80 cm. Each station was mounted on a frame with a connection for each sensor at each depth. Measurements were made bi-weekly during 13 months, starting in December 2005 and terminating in December 2006.

Calibration curves for each recording unit for soil moisture at each depth, season of the year, and forest type were made using a linear regression for the values of the sensors compared to those obtained by undeformed soil samples taken at the same depth of the sensors and drying them in a forced draft oven at 100 ºC until constant dry weight (direct method). The value of soil moisture in the direct method was obtained using the formula: θ = (soil wet weight/soil dry weight)-1, values in grams of water per grams of soil, or moisture based on mass weights ($g_{H2O}.g_{soil}^{-1}$) (Hillel 1971). Linear regression equations were used to obtain the value as the gravimetric percent of water ($g_{H2O}.g_{soil}^{-1}$) for each measurement.

Laboratory tests

To determine the principal hydraulic parameters of the soil, we collected undeformed soil samples in each area using a *Solotest* sampler (Solotest Equipamentos Ltda), with samples from the depths (0-5, 35-40,75-80 cm) in five profiles from each forest type (N = 45 for each forest type). Each sample was stored inside a stainless steel volumetric ring and maintained in closed aluminium tubes during transport to the soil physics laboratory of Embrapa-Cerrados (Planaltina-DF) for analysis. The parameters determined in this laboratory were: particle density, bulk density (BD), permanent wilting point (PWP), field capacity (FC), total porosity (TP), microporosity (MiP) and macroporosity (MP). The water holding capacity (WHC) was calculated by subtracting FC from PWP. The ratio between micro and macroporosity was calculated by dividing the value of the first by the second (MiP/MP).

The particle density was calculated dividing the oven dry weight of soil (g) by the volume of water displaced by soil (mL) (Tan 1996). The BD was determined using a volumetric ring (known volume of soil), where the value of the BD is obtained by the ratio of the mass of the volume of dry soil divided by the total volume of the soil, including particles and pores ($g\ cm^{-3}$) (Hillel 1971). Soil porosity was determined according to the EMBRAPA (1997) method: saturated samples in cylinders were placed under the tension table which removes water from macropores (pore 0.05 mm^3) by a tension of 60 cm of water column and then weighed. The samples were dried in an oven at 105 ºC and weighed to determine micropores by subtracting the first weight from the second and dividing the result by the volume of the cylinder. Total porosity is the sum of both. Aggregates (%) larger than 0.84 mm and smaller than 2 mm was determined

by a dry method, by passing soil samples in a standard sieve of 2 mm and subsequently in a standard sieve of 0.84 mm by electric stirrer assistance (EMBRAPA 1997).

Permanent wilting point and field capacity were determined by centrifugation by first saturating the soil with water, and then submitting the sample to six centrifugation cycles of 30 minutes, simulating tensions at different levels of atmospheric pressure (EMBRAPA 1997). The first cycle (6.07 kPa) corresponds to field capacity and the last (1519.87 kPa) to the permanent wilting point. Field capacity is related to the porosity and corresponds to the maximum benchmark of water holding capacity of the soil, and at this point the soil is saturated, while the permanent wilting point is the benchmark of minimum value, and below this point the majority of plants cannot absorb water from the soil (Hillel 1971). Although widely used as a benchmark for the minimum volumetric moisture in soil where plants are no longer able to extract water, permanent wilting point (-1.5 MPa) is a reference for cultivated plants (e.g. crops). Therefore, it is important to note that native tropical plants can extract water from the soil at tensions much lower than the -1.5 MPa (see Dunne & Wilmot 1996) traditionally referenced by soil-physics laboratories as permanent wilting point. However, we have decided to adopt this standard measure for comparisons with other studies, as well as to not differentiate from the standardization of soil hydraulics laboratories.

Hydraulic tests with the main tree species

We determined the minimum leaf water potential (Ψmin) for the six main important species that contribute over 60% of the total basal area in the mixed forest, and the monodominant species in the *Brosimum* forest (Jancoski et al, in preparation). The dominant and most important species (Importance Value Index – IVI) tested were *Brosimum rubescens*, *Tetragastris altissima*, *Amaioua guianensis, Chaetocarpus echinocarpus, Mabea fistulifera, Cheiloclinium cognatum* and *Ephedranthus parviflorus* for both forests (Marimon et al. 2001). Measurements were performed in August 2017 (peak of the dry season) between 12:00 and 2:00 pm. We measured five individuals of each species in 1-2 leaves using a pressure chamber (PMS Instruments Co., Albany, USA; model: 1505D-EXP; Scholander 1965). These leaves were mature, healthy looking, with no signs of senescence and exposed to the sun. The distance between each individual was at least ten meters.

Statistical analyses

The moisture and physical variables determined in the laboratory were compared between forests at each depth and each month using a t-test and through the year using Repeated ANOVA. To determine the correlation between the two forests in terms of soil moisture through the year we calculated the Spearman correlation for each depth. Since the Kolmogorov-Smirnov test (Sokal and Rolf 1981) indicated a non-normal distribution, data were log-transformed prior to the t-test (Zar 1999). The Ψmin was compared among species using a Kruskal-Wallis test and between areas using a t-tests with P-value ≤ 0.05 as level of significance. Spearman correlation tests were done using the program BioEstat 5.0 (Ayres et al. 2003), and all other statistical tests were done using Systat 7.0 (SPSS Inc. 1997).

Results

Annual variation in soil moisture

At 0-5 cm depth the soil in the BF had significantly higher soil moisture than the MF in all measurements throughout the year (Fig. 2). The soil moisture at this depth was above the permanent wilting point in both forests during the rainy season and below it during the dry season with an extreme dryness of the MF soil. The soil moisture was below field capacity at all three depths in all measurements (Table 2) in both forests during dry season. For this reason, the field capacity line is not present in figure 2.

At 35-40 cm depth in the BF, besides the minimal monthly variation in moisture content (12.3 to 13.0%), values remained below the permanent wilting point in all measurements. In contrast, soil moisture in the MF at this depth, as well as at 75-80 cm, was above the PWP during the entire rainy season and only fell below it during four months (June to September). The soil moisture in the MF varied from a maximum value of 17.7% in December 2006 to a minimum value of 11.0% in July 2006 at 35-40 cm depth. In contrast to the observations in the 0-5 cm layer, the MF had significantly higher soil moisture at the 35-40 cm depth than BF for almost all of the measurements. However, there was only a significant difference between forests at the 35-40 cm depth ($p \leq 0.05$) in January and September, probably as a result of a short dry spell in January and the end of the dry season in September when moisture sharply declines.

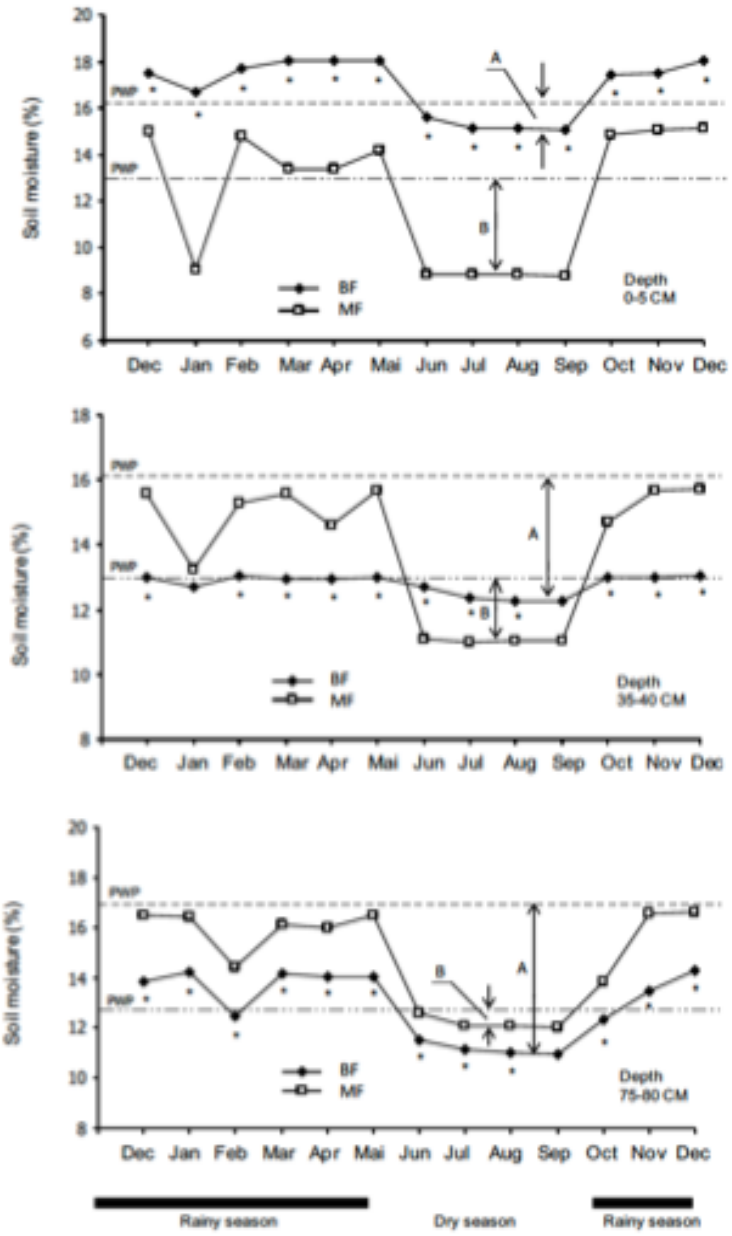

Figure 2 Monthly gravimetric soil moisture at each of three soil depths (0-5, 35-40, 75-80 cm) (average of 10 points) in the *Brosimum rubescens* monodominant forest (BF) and an adjacent mixed forest (MF) in 2005/2006, Nova Xavantina-MT. The arrows indicate the difference between the soil moisture and the permanent wilting point (PWP) of the BF (A) and the MF (B). *Significant difference between forests ($p \leq 0.05$).

At 75-80 cm depth, the soil moisture in the BF maintained the tendency observed in the other depths and was even farther from the PWP in all measurements. In the MF, however, the soil moisture was below the PWP in only four measurements (June to September), the period that corresponds to the peak of the dry season. The variation in soil moisture was always small in the BF, but slightly greater than that observed in the 35-40 cm depth. The highest value in the BF was 14.3% in December/06 and the lowest was 10.9% in September. The variation in the MF was slightly higher, with a minimum value of 12.0% in September and a maximum value of 16.6% in December/06. Similar to the 35-40 cm depth, the two forests had significant differences ($p \leq 0.05$) at almost all of the measurements with the exception of the month of September.

Despite significant differences in soil moisture at all depths, the seasonal pattern of variation in moisture was very similar in both forests (with more subtle variation in 35-40cm) as shown by the highly significant Spearman correlation, ($r_s > 0.7$; $p \leq 0.005$) for the three depths. Even the peaks of low soil moisture in January at the 0-5 cm and 35-40 cm depths and in February at the 75-80 cm depth were similar between forests.

Hydraulic tests of soil in the laboratory

The water retention curve determined in the laboratory was very similar between areas, with both having a reduction around 46% in water content at the first centrifugation stage (475 RPM = 6.07 kPa) (Fig. 3). The variation in water loss was practically identical for the other tensions used in the samples in both areas and three depths. In spite of the similarity in the intensity and form of the decay pattern of the curves, the BF had a higher variation in the range of saturation/drainage of the samples between ±50% to ±19%, a higher limit in relation to that observed in the MF (±38% to ±18%), considering all the depths from the first to the last trial.

The difference in moisture in the samples between the first trial (475 RPM, 6.07 kPa), that corresponds of field capacity (FC), and the last, that corresponds to the permanent wilting point (PWP), was very sharp, indicating a strong variation in water holding capacity (WHC) of the soil in both areas.

In the same way, the decrease in soil moisture between the saturation point and the field capacity was high in both forests (±45%), which also demonstrated a low water holding capacity. The calculated water holding capacity (WHC) was low in both forests, but lower in MF in all depths.

The bulk density was significantly higher in the MF, except at 35-40cm depth. However, the values of field capacity, PWP, microporosity, macroporosity and total porosity were significantly higher in the BF at all depths. The amount of gravel at the 35-40 cm and 75-80 cm depths was also higher in the BF. Despite significant differences in porosity between areas, there was no significant difference between area and depth for the ratio of macro to micropores (MiP/MP). The percentage of aggregates larger than 0.84 mm and smaller than 2 mm did not differ significantly between areas at any depth (Table 2).

Hydraulic tests of the main tree species

The minimum leaf water potential (Ψmin) of the seven main species in both forests ranged from -2.0 MPa (*Brosimum rubescens*) to -4.3 Mpa (*Amaioua guianensis*) (Table 3). Contrary to expected, none of the species differed between the two areas (including the monodominant), although four species differed from each other. In addition, the Ψmin of two species (*Tetragastris altissima* and *Mabea fistulifera*) was very similar to that of *Brosimum rubescens*. Other three species (*Ephedranthus parviflorus, Cheiloclinium cognatum* and *Chaetocarpus echinocarpus*) showed slightly more negative Ψmin than *Brosimum rubescens*, varying between 3.2 to 3.7 MPa.

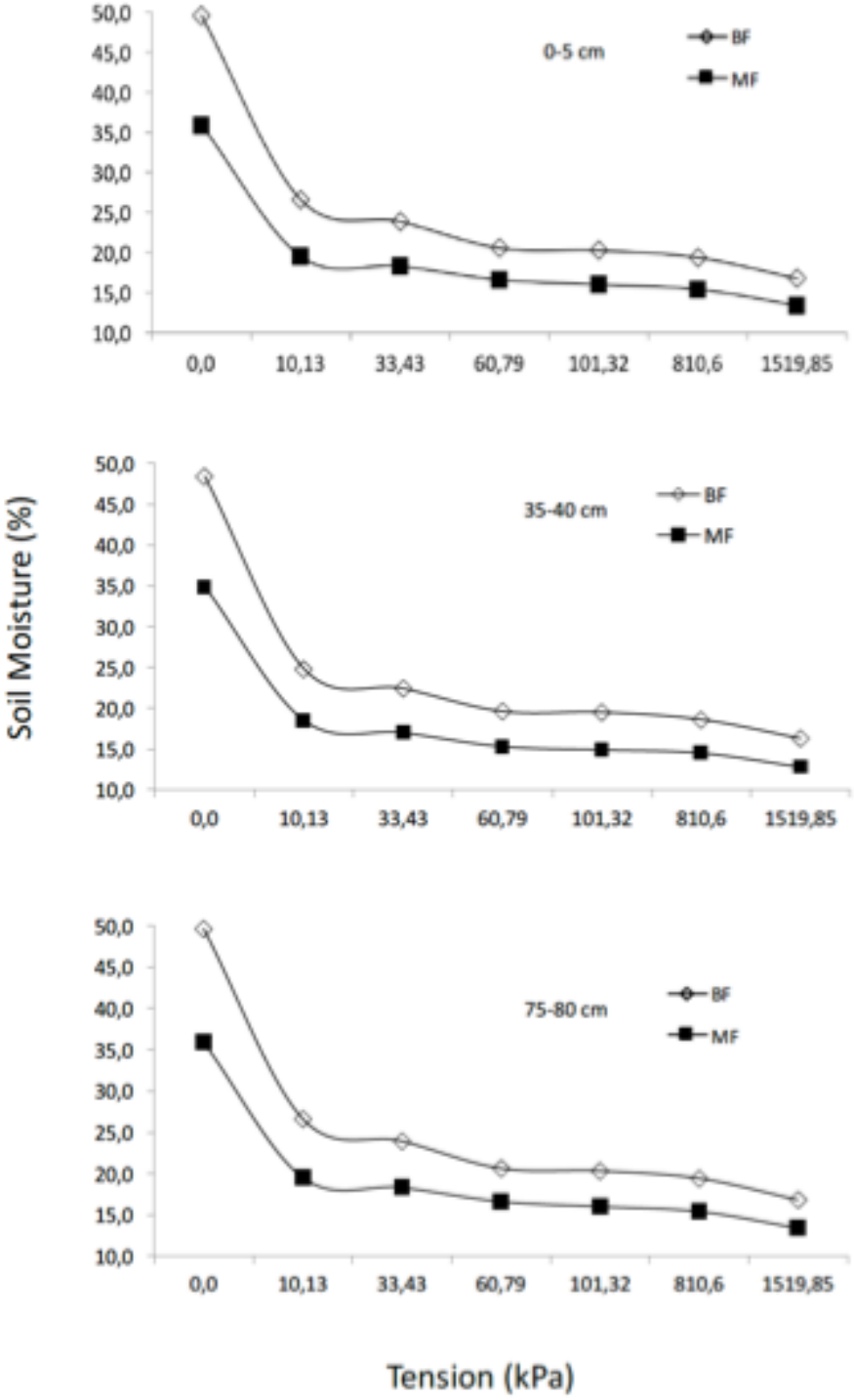

Figure 3 Water retention curves at three depths in the Brosimum rubescens (FB) monodominant forest and in the adjacent mixed forest (FM) in Nova Xavantina-MT. The values of kPa were simulated using different rotation velocities every 30 minutes in a centrifuge. The values in the X-axis represent ATM simulated in the centrifuge.

Table 2 Physical parameters of the soil in the *Brosimum rubescens* monodominant forest (BF) and the adjacent mixed forest (MF) in Nova Xavantina-MT. BD = Bulk Density; FC and PWP = % of water (V/V) corresponding to the Field Capacity and Permanent Wilting Point, respectively; WHC = Water Holding Capacity (FC-PWP); MiP = microporosity; MP = macroporosity; MiP/MP = ratio between micro and macroporosity; TP = Total Porosity; Gra (%)= percentage of gravel> 2 mm in diameter; Agg (%)= percentage of aggregates > 2 mm < 0.84 mm in diameter. FC, PWP and WHC expressed in volume of water per volume of soil (%) and bulk density in g cm^{-3}. Different letters indicate statistically significant differences between forests, at each depth within the same column ($p \leq 0.05$). Standard deviations are in italics.

Forest	Depth (cm)	BD	FC	PWP	WHC	MiP (%)	MP (%)	MiP/MP	TP (%)	Gra (%)	Agg (%)
BF	0-5	1.12a *0.09*	24.81a *4.02*	16.30a *1.83*	8.51a *0.87*	24.82a *4.01*	22.91a *3.68*	1.08a *0.12*	47.73a *5.68*	32.32a *3.95*	85.19a *12.8*
	35-40	1.09a *0.09*	24.69a *7.77*	16.25a *1.98*	8.44a *0.81*	24.67a *4.65*	23.65a *4.71*	1.04a *0.11*	48.32a *7.57*	56.82a *8.74*	91.11a *17.2*
	75-80	1.1a *0.19*	26.63a *6.30*	16.75a *2.18*	9.88a *0.89*	26.61a *6.30*	23.11a *9.51*	1.15a *0.13*	49.72a *10.83*	61.70a *9.65*	95.61a *21.9*
MF	0-5	1.24a *0.1*	19.51b *2.13*	12.91b *1.64*	6.6b *0.67*	19.49b *2.19*	19.01b *6.26*	1.02a *0.09*	38.53b *6.41*	30.93a *7.01*	76.83a *14.3*
	35-40	1.32b *0.12*	18.54b *2.2*	12.75b *1.48*	5.79b *0.71*	18.52b *2.23*	16.45b *3.81*	1.12a *0.10*	34.97b *4.12*	42.63b *6.85*	90.12a *13.6*
	75-80	1.31a *0.12*	19.56b *2.44*	13.47b *1.68*	6.09b *0.68*	19.46b *2.52*	16.36b *4.63*	1.19a *0.14*	35.79b *4.91*	47.27b *8.91*	91.47a *17.4*

Table 3 Minimum leaf water potential (Ψmin) for the seven main species (relative dominance, basal area) of the *Brosimum rubescens* monodominant forest (BF) and the adjacent mixed forest (MF) in Southern Amazonia, Nova Xavantina-MT.

Species (family)	**$\Psi_{min\ (MPa)}$**
Brosimum rubescens (Moraceae)	-2,0
Ephedranthus parviflorus (Annonaceae)	-3,7
Chaetocarpus echinocarpus (Peraceae)	-3,2
Tetragastris altíssima (Burseraceae)	-2,4
Amaioua guianensis (Rubiaceae)	-4,3
Mabea fistulifera (Euphorbiaceae)	-2,6
Cheiloclinium cognatum (Celastraceae)	-3,3

Discussion

Water retention curves and hydraulic parameters of soil and plants

We hypothesized that a more restrictive soil moisture environment in BF would be related to the monodominance of *B. rubescens*. However, contrary to expectations our results showed significantly better conditions in soil water holding capacity (WHC) and other hydraulic parameters for BF compared to the MF in the soil profile. Nevertheless both areas showed low WHC (<10-20% $cm^3_{H2O}.cm^{-3}_{SOIL}$) compared to other areas in the Cerrado and Amazon (~19-42 $cm^3_{H2O}.cm^{-3}_{SOIL}$) (e.g. Jipp et al. 1998; Oliveira et al. 2005; Juhász et al. 2006) and high variation of the water retention curves, which may be the result of the large amount of gravel in the soil profile, as discussed below. In addition, the fact that *B. rubescens* leaf water potential (Ψmin) did not differ between areas evidences that the monodominant species is not experiencing more water stress than trees in the mixed forest. Furthermore, the water potential of two species (*Tetragastris altissima* and *Mabea fistulifera*) was similar to that of *B. rubescens*, revealing that the monodominant species is not the only one to have this hydraulic behaviour.

Such conditions clearly suggest that the monodominant species does not have a competitive advantage in the sense of resisting hydraulic stress compared to the other species of importance in the communities in both forests. Therefore, we reject the hypothesis that monodominance of *B. rubescens* is primarily determined by low WHC in the monodominant forest and hydraulic advantages of the monodominant species. This is consistent instead with the idea that tropical forest monodominance is not determined by a single factor. In the case of our forests other factors must be at play instead. For example, the low Ca/Mg ratio of BF (Table 1) is remarkably unfavourable in terms of fertility, with values below those normally registered in tropical soils (e.g. Quesada et al. 2012). These soil chemical conditions may contribute to a wider set of environmental characteristics that could determine the monodominance in tropical forests (e.g. Nascimento et al. 1997; Marimon et al. 2001, Nascimento et al. 2017).

Despite the differences in WHC, the hydraulic curves revealed that both areas have low water retention capacity, which restricts the water balance of plants in these marginal climates for tropical forests. This is clear in the abrupt variation of soil moisture, represented by the drop peaks of humidity and the slope of the curves in the laboratory tests. The water retention curves in the soil of the BF and MF, at all three depths, had a steep slope higher than many neotropical soils under native or managed vegetation (e.g. Reis and Rassini 1986; Jipp et al. 1998; Spera et al. 2000; Oliveira et al. 2005; Juhász et al. 2006), probably due to the high gravel concentration, which cause low water retention (Lopes 1984). This also explains the low water availability capacity in both areas. Besides the gravel content, other edaphic factors such as density, micro and macroporosity also influence water retention and availability in the soil profile (Hillel 1971; Brady and Weil 1996). However, the values of these parameters, including the ratio between micro and macroporosity, are not remarkable, all being close to the mean values recorded for soils under native vegetation in Brazil (e.g., Spera et al. 2000; Araújo et al. 2004).

The greater percentage of gravel in the BF at the depths of 35-40 and 75-80 cm may be the cause of the lower moisture levels in the BF in these depths compared to the MF and may also explain the water percentage below the permanent wilting point (PWP), in contrast to our observations for the MF soil, which had normal hydraulic behaviour (Figure 2). Ivanauskas (2002), working in a transition forest in the same region of BF and MF in eastern Mato Grosso, found values above the PWP during the greater part of the year in similar depths to that of the MF, and oscillating around field capacity during the rainy season, a result that was not observed during the rainy season in either forest in our study.

Monthly and annual variation in soil moisture

The moisture distribution in the soil profile in the MF had practically the same behaviour in the dry and rainy seasons, with the percentage of moisture increasing with depth up to 75-80 cm, that could also be observed in other soils, such as observed by Quesada et al. (2004) in a field in the Federal District (Brazil), with higher values of water at deeper levels, in both the rainy and

dry seasons. This was also observed by Lopes (1984) in a cultivated area on a Dark Red Latosol and by Oliveira et al. (2005) in dense cerrado and field in the Federal District. Ivanauskas (2002) verified the same pattern in a transitional forest in eastern Mato Grosso during most of the year except at the end of the rainy season when the superficial layers of the soil had a higher water content.

The highest water value in the superficial layer of the BF may be related to diverse physical factors that are associated with soil hydrology and/or intrinsic biotic factors associated with the vegetation and its hydric relations in the soil-plant-air continuum (e.g. transpiration rates) (Taiz and Zeiger 1998). The first option is not probable, since the amount of gravel, aggregates, bulk density, microporosity (MiP), macroporosity (MP) and ratio MiP/MP did not significantly differ between forests.

The field capacity and permanent wilting point (PWP), despite being significantly different, had the same behaviour in both areas at all depths, indicating that there was no important physical factor in soil hydrology that would differentiate the superficial layers from deeper layers in either forest. An alternative explanation for this case could be related to the soil-root relationships. For example, this soil layer is in direct contact with the superficial root mat and litter layer and can be influenced by both. However, the moisture of the litter layer is the same in both forests (Marimon-Junior 2007), eliminating the influence of the moisture in the litter layer on the superficial soil. Another explanation for this higher moisture in the 0-5 cm layer in the soils in the BF may be related to hydraulic lift (Richards and Caldwell 1987). This layer is in direct contact with the superficial root layer and may be receiving water from *Brosimum rubescens*, in the case that this species is capable of hydraulic lift, as shown for some tree species in the *Cerrado* biome (Franco 2005). According to that study, this phenomenon generally occurs at night when the water potential of the roots exceeds the water potential of the dryer soil layers as a consequence of diminished transpiration. In this case part of the water extracted by the roots from deeper soil layers is lost to the higher superficial layers (Richards and Caldwell 1987), a process that might benefit the mineral nutrition of the monodominant species. However, to assess this hypothesis it would be necessary to develop studies of the daily patterns of sap flow and other manipulative experiments (e.g., Scholz et al. 2002).

Despite absolutes values of soil moisture being significantly different between forests throughout the year, the monthly pattern of variation (moisture curve, Figure 2) was quite similar between the BF and the MF. This synchrony probably is due to the similarity of the soils in relation to the distribution of micro/macroporosity, gravel, aggregates and soil density over the soil profile. Thus, the variation in these values between one layer and the other is similar in both forests, a pattern also verified for all the other physical-hydrological parameters. Since these parameters determine the hydraulic behaviour of the soil, and the annual rainfall is the same for both forests, the annual variation in moisture should also tend to be the same in both forests.

Soil moisture and monodominance

We had hypothesized that under soil water restriction *B. rubescens* could be a better competitor than the other species and thus attaining monodominance. However, we find two situations that rule out our hypothesis. First, *B. rubescens* did not show differences of Ψmin between the two areas, with minor differences between at least two other main species (IVI) of both forests. Second, our field results revealed that soil water conditions in the BF are in fact no more restrictive than in MF. Contrary to expectations, the soil moisture variations of BF in field reveals not a disadvantage but a slight advantage in terms of water availability for the plants, possibly due to the differences in soil gravel content between the forests not being great. Taken together, our results imply that soil physical differences probably are not so great as to drive the floristic and structural differences between the two vegetation, and certainly cannot drive the monodominance of *B. rubescens*.

Therefore, one alternative explanation for monodominance in this case could be possible other hydraulic conditions not determined in this work, as high water transport efficiency (Meinzer et al., 2009), which promotes hydraulic advantages to the monodominant species, especially on the BF soils that have a slight moisture advantage. For example, Bittencourt et al.

(2016) suggested the existence of other axes of hydraulic traits affecting the plant water balance, such as hydraulic space-use efficiency in the wood tissue. The authors named this set of anatomic-functional traits as *Ks*, which is directly correlated with leaf water supply capacity, allowing plants to operate under higher water potentials, and consequently, to survive with hydric restrictions. Thus, we propose here future investigations on hydraulic efficiency traits of *B. rubescens*, such as fibres and conduit wall space allocated to conductance as implosion–efficiency trade-offs, or parenchyma space allocated to conductance, which may be related to refilling efficiency or to water supply by capacitance (Bittencourt et al 2016). Such investigation, aside from estimations of the root depth of *B. rubescens*, could provide clues for a better understanding not only of the monodominance, but the soil-hydraulic drivers of plant species distribution and dominance in tropical ecosystems (e.g. Esquivel-Muelbert et al., 2016).

The soil-water patterns observed in field were corroborated by the laboratory tests. The water retention curves were practically identical for soil of both forests and depths, indicating lower water retention capacity compared to other types of soils under forest, cerrado, field or even pasture (e.g., Reis and Rassini 1986; Jipp et al. 1998; Spera et al. 2000; Oliveira et al. 2005; Juhász et al. 2006). Despite this restriction, it is possible to observe a high percentage of species with new leaf buds in both forests even at the height of the end of the dry season, and also the presence of seedlings. This is common in these Amazon/Cerrado transitions, since many tree species of the Amazon forest absorb water deep in the soil (Nepstad et al. 1994; 1995), maintaining transpiration rates (Carvalheiro and Nepstad 1996), and allowing them to survive long dry spells (Nepstad *et al.* 2002).

We hypothesized that differences in soil moisture restriction between *Brosimum* and mixed forest would be sufficient to influence monodominance. As this did not occur to a high degree, we suggest two possible explanations. The first is that the BF itself might have influenced the hydraulic properties of the soil (e.g., hydraulic lift). The second is that the observed differences in the physical parameters of the soil were not sufficient to produce greater differences in the water retention capacity of the soils. If the first hypothesis is correct, potentially hydraulic properties would be influenced via potentially enhanced species-specific hydraulic lift of *Brosimum rubescens*, an aspect that was not investigated in the present study. If the second hypothesis is correct, further studies of soil physics are necessary in the field and laboratory.

Therefore, our results indicate that soil water holding capacity and surface water availability in BF are not clear determining factors of monodominance on their own even with values below the permanent wilting point in the deeper soil layers. However, another environmental situation that should be investigated is the depth of the water table in the two areas to verify possible differences in the availability of deep soil water. According to other studies conducted in the BF, monodominance may also be related to the high Mg:Ca ratio in the soil (Marimon et al. 2001), and associated with another ecological and life-strategy characteristics, such as the extensive seedling bank of *B. rubescens* and its plasticity in relation to light conditions (Marimon et al. 2008), which permit the maintenance of the population through multiple gap opening events (Marimon et al. 2012).

The causes of classical monodominance (*sensu* Connell and Lowman 1989 and Peh et al. 2011b) remain generally uncertain in the tropics. In our case, further investigation is needed into mechanisms not only related to physico-chemical properties of soils but mainly on the ecophysiological traits of *B. rubescens* (e.g. wood anatomy and root depth). In this sense, in addition to the ecophysiological factors discussed here, future research should also focus on that proposed by Marimon (2005) and Marimon et al. (2012), where the monodominance of *B. rubescens* is attained by a complex mechanism involving formation of a persistent seedling bank (see also Nascimento and Proctor 1997) in conditions of long-term cycles of gaps openings under a very-shaded canopy.

Conclusions

The dominance of *Brosimum rubescens* is not directly related to the physical properties of soil, since the water retention curve for both forests has the same pattern, in spite of some restrictive physical conditions, such as higher total porosity and gravel proportion. The fact that the extreme concretionary (gravel) nature and low water holding capacity of the soil is not the main factor determining monodominance of *Brosimum rubescens* reinforces the idea that tropical monodominant forests are determined not by a single factor, but a set of ecological conditions acting in concert, as initially proposed by Connell and Lowman (1989).

We can also consider other plant hydraulic conditions, such as high water transport efficiency promoting hydraulic advantages to the monodominant species, especially on the BF soils that have a slight moisture advantage. Similarly, other axes of hydraulic traits, like hydraulic space-use efficiency in the wood tissue, can be proposed as future investigations on hydraulic efficiency of *B. rubescens*, aside from root depth. These new trends of studies open up new possibilities for better understanding of the causes and consequences of tropical monodominance and the environmental drivers of tree species dominance.

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